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THE SEXUALLY DIMORPHIC JAMMING AVOIDANCE RESPONSE IN THE ELECTRIC FISH *EIGENMANNIA* (TELEOSTEI, GYMNOTIFORMES)

BY BERND KRAMER

Zoological Institute of the University, D-8400 Regensburg, Federal Republic of Germany

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SUMMARY

Eigenmannia's jamming avoidance response (JAR) is a frequency change of its electric organ discharge (EOD) in response to an electric stimulus of similar frequency (small ΔF; $\Delta F = F_{Fish} - F_{Stim}$). It is assumed that the response to an unclamped stimulus, $\Delta R = F_{Response} - F_{Rest}$, is stereotyped and non-habituating, and improves the fish's electrolocation performance in the presence of a jamming stimulus, such as the EOD of a nearby conspecific.

Adult females gravid with eggs ($N = 3$) gave good responses (frequency decrease of at least 3 Hz) to $-\Delta F$ (stimulus frequency higher than fish frequency), but no response or only weak responses (<0·5 Hz) to $+\Delta F$ (stimulus frequency lower than fish frequency). After 2·75 years, a sexually mature female still showed the same behaviour, whereas an immature female (see below) had changed its behaviour considerably on becoming sexually mature.

Large males ($N = 4$) did not give JARs to $+\Delta F$, and no JARs or only weak ones to $-\Delta F$ ($|\Delta R| < 0{\cdot}7$ Hz). Increasing the stimulus intensity by +10 or +20 dB did not change this result. After 2·5 years, two large males were still found to be almost unresponsive. However, large males gave rapid frequency modulations ('short rises' and 'interruptions'), which have been described from threatening fish likely to attack, even at the weakest stimulus intensity.

One group of juveniles ($N = 4$; probably females) gave only a weak increase in frequency ($\Delta R < 0{\cdot}9$ Hz) in response to $+\Delta F$ but a strong frequency decrease ($|\Delta R| > 2$ Hz) in response to $-\Delta F$. Another group of juveniles ($N = 4$; probably males) gave strongest responses ($\Delta R > 3$ Hz) to $\Delta F = 0$ Hz. In these juveniles, the 'equilibrium point' of no response was at $\Delta F \approx -0{\cdot}6$ Hz to -1 Hz instead of at $\Delta F = 0$ Hz. They thus increased, rather than decreased, their EOD frequency even at small $-\Delta F$s, which would have been more economical. A decrease in frequency was weaker than an increase. A significant frequency change could even be elicited by stimuli of $\Delta F = 0$ Hz that are phase-locked to the EOD.

The accuracy of assessment of ΔF, as determined in juvenile fish giving good $+\Delta R$s and $-\Delta R$s, was not better than $\pm 0{\cdot}3$ Hz (at $\Delta F = -0{\cdot}6$ Hz). The JAR showed strong habituation.

Dedicated to Professor Kurt Fiedler on his 60th birthday.

Key words: jamming avoidance response, electric organ discharge, frequency difference, beat frequency, sexual dimorphism, *Eigenmannia*.

None of the 14 fish showed a frequency difference *vs* response curve close to optimal for the purpose of jamming avoidance. An alternative function of the JAR in social communication is considered.

INTRODUCTION

The tropical South American knife fish *Eigenmannia (Sternopygus) lineata* (Mueller & Troschel), like other *Eigenmannia*, discharges its weak electric organ in a continuous, wave-like manner. Hence, *Eigenmannia* is a 'wave fish' and not a 'pulse fish' like the electric eel or the African Mormyridae, whose discharges resemble muscle or nerve action potentials separated by relatively long intervals of no potential difference.

Within a species-characteristic range of about 260–650 Hz the electric organ discharge (EOD) frequency of an individual *Eigenmannia* is remarkably constant at stable temperatures (Watanabe & Takeda, 1963; Bullock, Hamstra & Scheich, 1972*a*). The EOD frequency is not normally affected by vibration, sound, light or salinity changes (Bullock *et al.* 1972*a*; Kramer, Tautz & Markl, 1981).

Watanabe & Takeda (1963) discovered a 'peculiar response': when stimulated with a weak electric signal ($>3\,\mu V\,cm^{-1}$) close to its own EOD frequency, *Eigenmannia* changed its frequency 'as if to escape from the applied frequency'. With a stimulus frequency higher (or lower) than the EOD frequency, the fish lowered (or raised) its EOD frequency. The effectiveness of the stimulus depended on the frequency difference, ΔF: the smaller the difference the more effective the stimulus. The response only failed to occur 'when ΔF was very close to zero' (see Fig. 1, redrawn from Watanabe & Takeda, 1963; Larimer & MacDonald, 1968).

Watanabe & Takeda (1963) assumed the function of *Eigenmannia*'s response to frequencies close to its own was to enable the fish 'to distinguish between its own signal and those of its neighbours' for better object detection. However, electrolocation performance suffered only at high stimulus intensities close to the fish's own near-field EOD intensity (see review by Heiligenberg, 1977).

The response was investigated in greater detail by Bullock *et al.* (1972*a*,*b*) and Scheich (1977*a*), who called it the 'jamming avoidance response' (JAR). The optimal ΔF eliciting strongest responses was about ± 3 Hz when using a frequency-clamping technique devised to hold ΔF dynamically constant, frustrating the normal escape response from the jamming frequency. This is considerably more than the minimum effective ΔF of below 0·2 Hz (Bullock *et al.* 1972*b*), or the optimal ΔF with an unclamped stimulus (0·2–0·5 Hz according to Watanabe & Takeda's plot of Fig. 1).

The convergence of electrosensory input on a single output (the medullary pacemaker; Szabo & Enger, 1964) governing a quantifiable behaviour occurring in social encounters has stimulated attempts to identify the effective stimulus parameters and the nature of sensory coding and of the correlated central responses (Scheich, 1977*a*,*b*,*c*; see review by Heiligenberg, 1986). These efforts, along with neuroanatomical studies (see reviews by Scheich & Ebbesson, 1983; Heiligenberg, 1986), have resulted in neural models of the JAR based on the notion of time domain

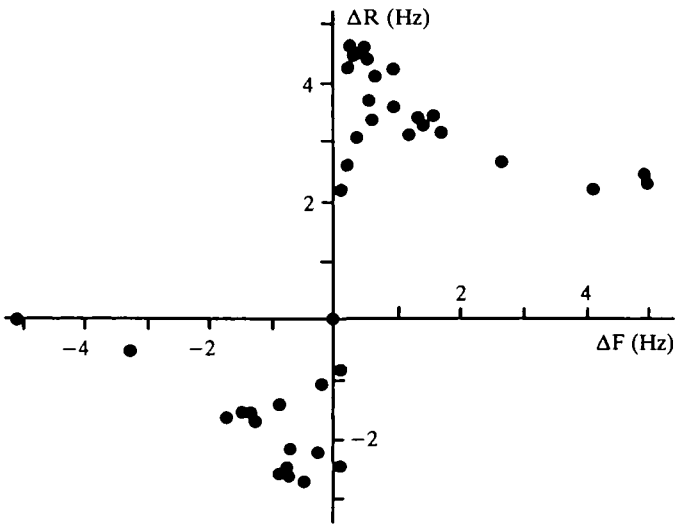

Fig. 1. The frequency difference *vs* response curve of one *Eigenmannia* as observed by Watanabe & Takeda (1963; redrawn from their fig. 4). The response is measured as the frequency change, $\Delta R = F_{Response} - F_{Rest}$ (Hz). The frequency difference between the fish's resting EOD and the stimulus is $\Delta F = F_{Fish} - F_{Stim}$ (Hz). With the stimulus frequency higher or lower than the fish's resting frequency, the fish lowered or raised its frequency, respectively, increasing the frequency difference. No response was observed at $\Delta F = 0$ Hz.

mechanisms of ΔF assessment, as opposed to true frequency analysis (Scheich, 1974).

Recent JAR experiments using digitally synthesized natural and artificial stimuli (Kramer & Weymann, 1987), including *Eigenmannia*'s sexually dimorphic EOD, have shown that the response strength (measured as frequency change in Hz) depends on the spectral composition of a stimulus, and *not* on its waveform (Kramer, 1985). Response strength was correlated with the intensity of the stimulus harmonic that was within a narrow frequency band centred on the fish's EOD frequency (equivalent to a limited spectral amplitude, or Fourier analysis). This type of signal analysis should be expected from the known properties of *Eigenmannia*'s tuberous (high-frequency) electroreceptors (especially P-receptors; but see Viancour, 1979*a*, who only found one type) which resemble broad bandpass filters approximately tuned to the EOD fundamental frequency (Scheich, Bullock & Hamstra, 1973; Scheich, 1977*b*; Hopkins, 1976; Viancour, 1979*a*,*b*,*c*).

Little work on the JAR has been done with unclamped stimulus frequencies, except the pioneering study by Watanabe & Takeda (1963) and the studies by Larimer & MacDonald (1968) and Kramer (1985). An unclamped stimulus frequency allows the fish to show its normal escape response, which may or may not be in the direction that would be enforced by the frequency difference clamp. Active frequency following is a type of interaction unknown in nature [see Bullock *et al.* (1972*a*) for evidence on two-animal interactions].

Great inter-individual variability in JAR behaviour between sex and age groups, including responses in the opposite direction to those observed in earlier work, was found, and this cannot be explained by present theory (Kramer, 1985). Therefore, a separate and more complete analysis into this variability has been carried out.

MATERIALS AND METHODS

Fourteen *Eigenmannia* (8·7–37 cm, Fig. 2; identified as *E. lineata* by F. Kirschbaum), imported from South America by a local fish dealer (at below 12 cm; probably from Leticia, Colombia, on the Amazon river), were kept together in the laboratory in planted 360-1 aquaria ($27 \pm 0{\cdot}5$ °C, conductivity 100–1000 $\mu S\,cm^{-1}$). The animals were sexed by visual inspection of the gonads through the translucent skin according to F. Kirschbaum (personal communication), and by a sexual dimorphism in EOD waveform and intensity, and body size (see Kramer, 1985). The EOD waveform character was measured by the P/N ratio, which is the ratio of intervals between zero-crossings of the head-positive and the head-negative half-waves of one EOD cycle. Young fish start with almost sinusoidal EODs characterized by high P/N ratios of $>0{\cdot}8$ (as also evident from oscilloscope tracings of larval EODs; Kirschbaum & Westby, 1975); adult females show P/N ratios of $\geq 0{\cdot}6$, and adult males of $<0{\cdot}6$ (as low as 0·4).

The experimental aquarium (52×25×28 cm high; conductivity $100 \pm 5\,\mu S\,cm^{-1}$; $26{\cdot}7 \pm 0{\cdot}2$°C) was provided with a porous pot (length, 17·5 cm; inner diameter, 3·3 cm; wall, 0·3 cm) open at one end. For large individuals a porous pot of greater size was provided (length, 33 cm; inner diameter, 6·5 cm; wall, 1·2 cm). The experimental aquarium was placed in a larger tank (80×50×50 cm high) the grounded tapwater of which was heated; both tanks were aerated. Mechanical disturbances from the floor of the building were attenuated by air-cushions underneath the feet of the experimental table. The fish were placed in the experimental aquarium at least 2 days before experiments started; they remained there until all experiments were completed (within a few weeks).

The experiments were performed during daylight hours only (L:D, 12 h:12 h), when the nocturnal fish remained in their dark porous pots. To prevent the fish from accidentally leaving the shelter, its opening was covered by coarse plastic mesh. The fish were set free and fed on frozen *Chironomus* larvae before dark.

The EODs were differentially recorded head-to-tail by a pair of carbon rod electrodes (3·3×0·4 cm) connected to a wideband preamplifier (100 kHz). The EOD frequency was measured under microcomputer control (Hewlett Packard model 85A) using an electronic counter (Hewlett Packard model 5308A) in the 'period average' mode (averaging of 10 EOD cycles) accurate to 0·0004 % (or 0·002 Hz at 400 Hz). In any experiment, the EOD frequency was measured twice per second for a period of 2 min. The resting or baseline EOD frequency of the unstimulated fish was determined as the average of 120 measurements during the first minute and thus represents 1200 EOD cycles. During the second minute, the stimulating field

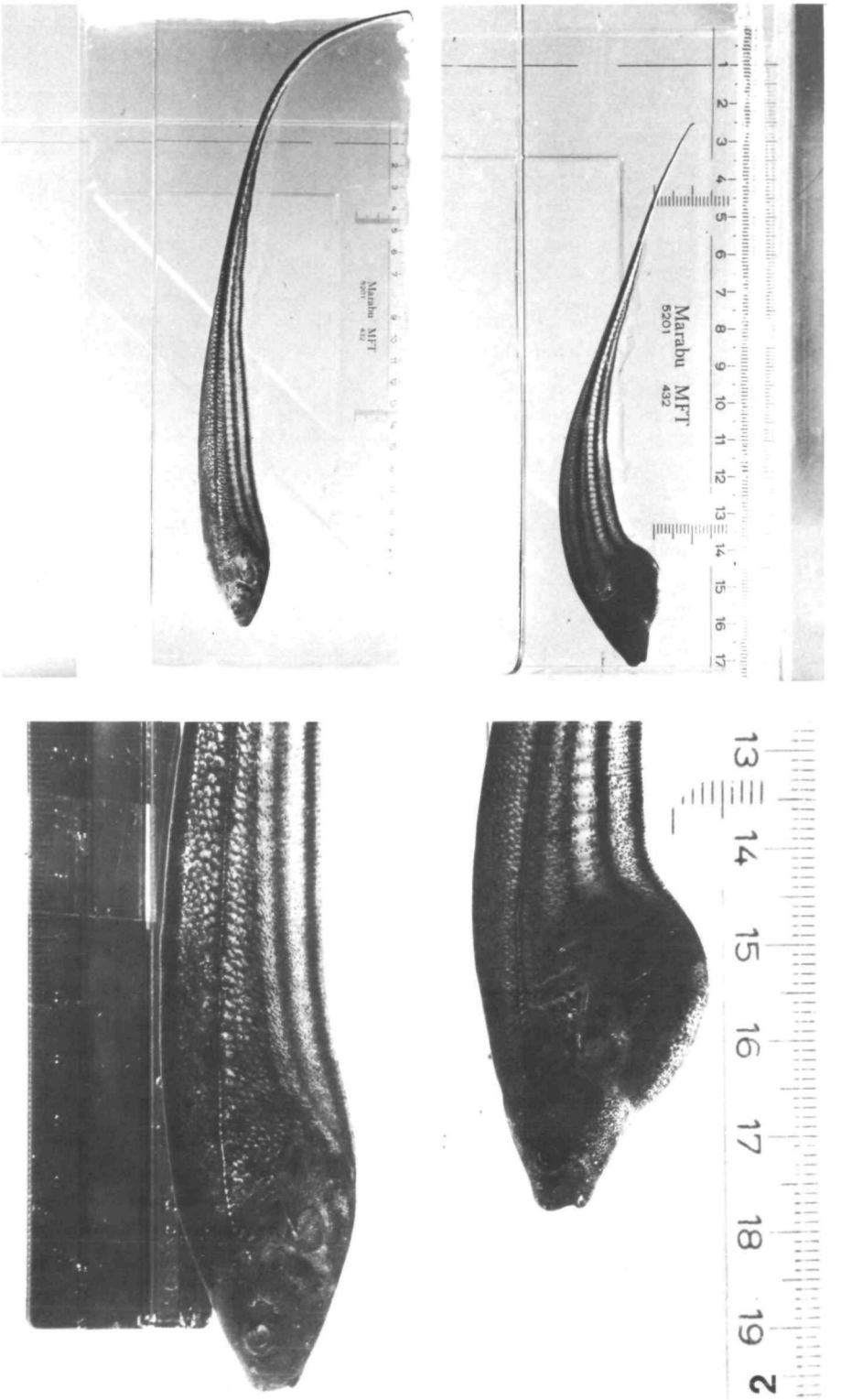

Fig. 2. An adult male (upper two photographs) and an adult female (lower two photographs) *Eigenmannia lineata*.

($29{\cdot}6\,\mu V_{P-P}\,cm^{-1}$ = standard stimulus intensity) was applied across the fish by a pair of carbon rod electrodes positioned symmetrically, approximately opposite the middle of the fish. The stimulus electrodes were separated from the stimulus generator by an isolation transformer (100–18 000 Hz).

The sinusoidal stimulating field (rise time 400 ms; higher harmonics at least −60 dB) was generated by a synthesizer/function generator (Hewlett Packard model 3325A) connected to the controlling computer. The stimulus frequency, F_{Stim}, was automatically adjusted to the preselected frequency difference value, ΔF ($\pm 0{\cdot}01$ Hz), by computer on-line to the experiment ($\Delta F = F_{Fish} - F_{Stim}$). The response magnitude of the JAR, $\Delta F = F_{Response} - F_{Rest}$, was measured as the mean frequency change 40–60 s after stimulus onset when the EOD frequency had normally reached a plateau (see fig. 1 in Kramer, 1985). As the stimulus frequency remained fixed, the fish could increase the frequency difference continuously until its EOD reached a new 'equilibrium' frequency.

Twelve experiments per fish were run at each ΔF; the inter-trial interval, Δt, was 20 min since with shorter intervals (or at higher stimulus intensities) habituation occurred (Fig. 3; see also Kramer, 1985).

Statistical tests were calculated according to Siegel (1956) and Sachs (1978); all *P*-values are two-tailed.

RESULTS

Frequency–response curves for juvenile to subadult immature fish

Some of the fish used for these experiments, for brevity referred to as juveniles, were close to or within the group size of adult females (about 15–18 cm), but much smaller than adult males which are often >30 cm. All of these 'juveniles' (nos 1–8) had P/N ratios of >0·6, which is typical of females and of immature fish. Thus, they were clearly not adult males (by their small size and their high P/N ratios), nor did they belong to the group 'adult females gravid with eggs' (because of their undeveloped gonads and, in most cases, smaller size).

Two of the three juveniles tested (nos 3 and 4, Fig. 4; but not no. 8, Fig. 5) showed small, but significant, responses ($P < 0{\cdot}05$; *t*-test), even at $\Delta F = +20$ Hz, in the direction predicted from the results of Watanabe & Takeda (1963). At $\Delta F = -20$ Hz, only juvenile no. 3 gave significant responses ($P < 0{\cdot}001$); there were no responses to $\Delta F = \pm 30$ Hz or ± 40 Hz ($P > 0{\cdot}05$).

In contrast to earlier observations, juveniles nos 1–4 showed strongest (or nearly strongest) responses to stimuli of no frequency difference ($\Delta F = 0$ Hz); hence, $\Delta F = 0$ Hz was the most effective stimulus in these fish (Fig. 4). Juveniles nos 1–4 responded by an increase in frequency as long as the stimulus frequency was below, or not more than about 0·5 Hz (occasionally even 1·5 Hz, juvenile no. 4) above, their own frequency. In increasing their frequency, these fish first *reduced* ΔF and then passed over the stimulus frequency, before they could start to increase ΔF (an

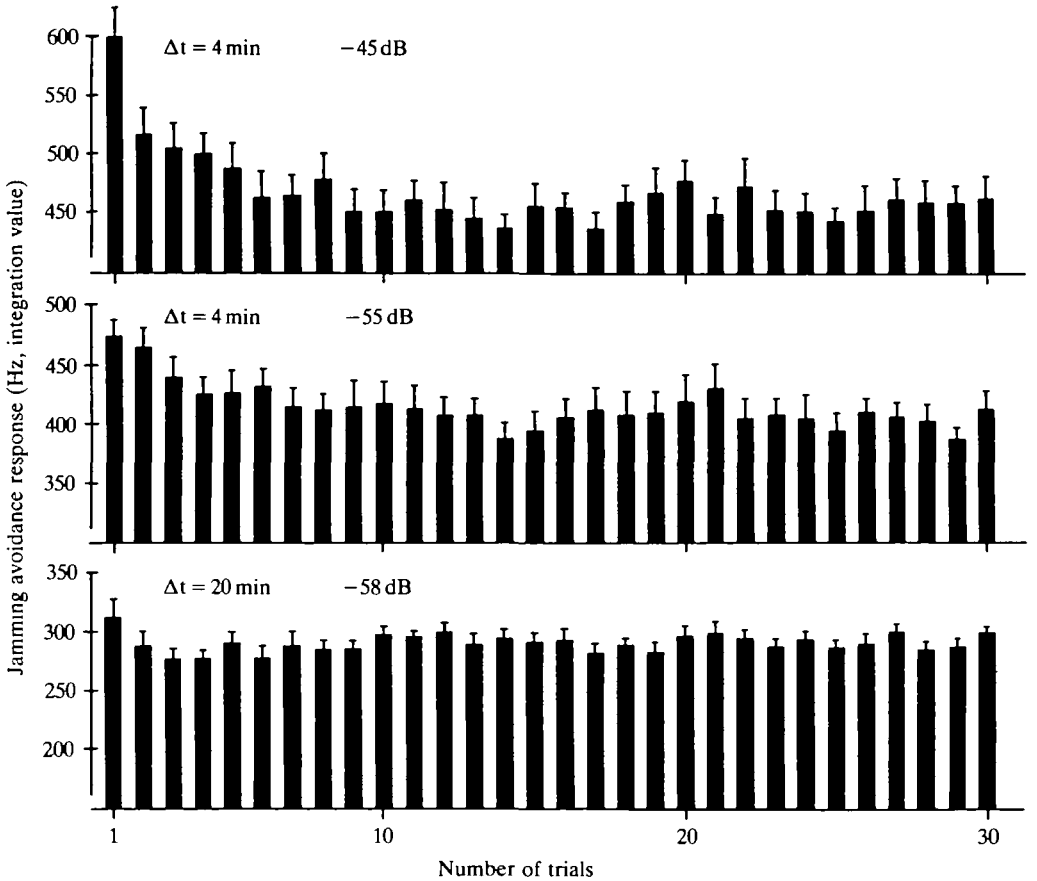

Fig. 3. Habituation of JAR is stronger the higher the stimulus intensity (dB re: 29·6 $mV_{P-P}\,cm^{-1}$) and the shorter the inter-trial interval (Δt). JAR is shown as the mean integrated frequency change (+1 S.E., $N = 10$) relative to the baseline frequency (during 60 s of stimulation). Thirty experiments per day were run on 10 successive days (starting at the same time each day). *Eigenmannia lineata*, adult female no. 1 at ΔF = −2 Hz. No habituation was detectable at Δt = 20 min and weakest stimulus intensity (−58 dB; lower diagram: Spearman rank correlation coefficients, r_s, were insignificant for the first 3, 4, 10, or all trials; $P > 0{\cdot}05$). Strong habituation was detected for the first 10 trials at Δt = 4 min and highest stimulus intensity (−45 dB; upper diagram: $r_s = -0{\cdot}445$; df = 98; $P < 0{\cdot}0001$) and for the first 10 trials at Δt = 4 min and weaker stimulus intensity (−55 dB; middle diagram: $r_s = -0{\cdot}353$; df = 98; $P < 0{\cdot}001$). In none of the diagrams was habituation detected on analysing trials 11–30 (all r_s values insignificant, $P > 0{\cdot}05$; df = 198 in each case).

example showing the time course of one such response is given in Fig. 6). In these fish, an increase in frequency was stronger than a decrease.

In response to negative and positive ΔFs of the same absolute value, the fish changed their frequency such that they obtained about the same frequency difference (this is especially clear in juvenile no. 3).

Juveniles nos 5–8 behaved differently from juveniles nos 1–4. In these fish, ΔF = 0 Hz was ineffective, and maximum positive ΔR values were considerably

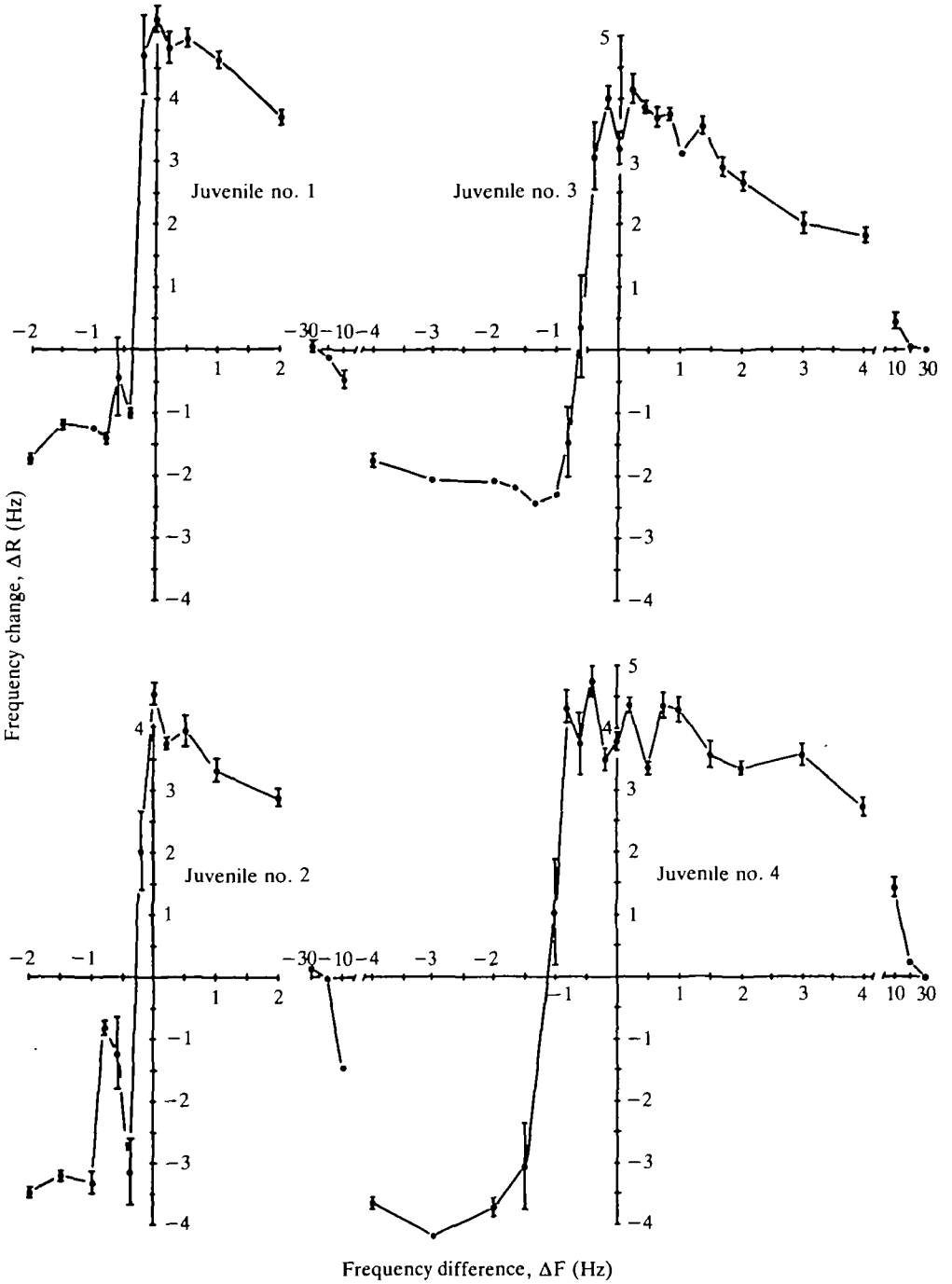
Juvenile no. 1
Juvenile no. 3
Juvenile no. 2
Juvenile no. 4
Frequency change, ΔR (Hz)
Frequency difference, ΔF (Hz)

Fig. 4

smaller than negative ones (Fig. 5). Frequency increases in response to positive ΔF values barely exceeded a meagre 0·5 Hz, as opposed to 2 Hz or more in response to negative ΔF values.

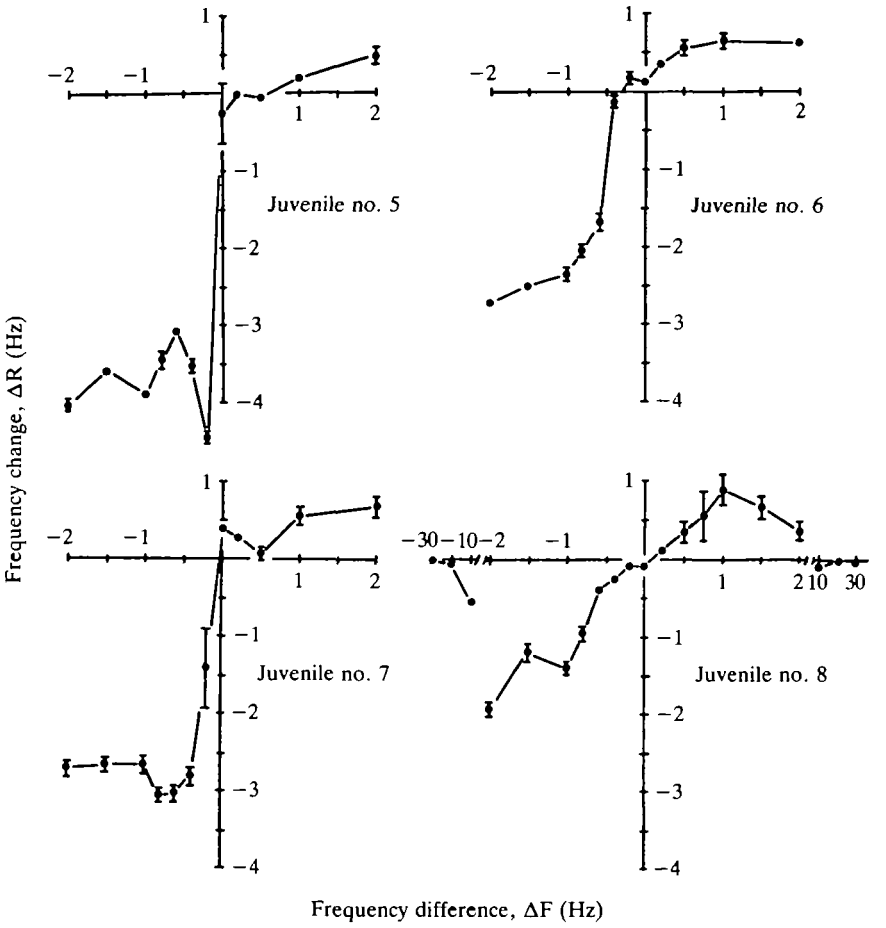

Fig. 5. Frequency difference *vs* response curves of four juvenile (or subadult) *Eigenmannia lineata*. ΔR and ΔF as defined in the legend to Fig. 1. These fish gave only weak responses to stimulus frequencies lower than their own (+ΔF), while −ΔFs evoked good responses. Each point is a mean ± 1 S.E. ($N = 12$). Standard errors are either shown or are too small to be drawn. Standard stimulus intensity. Body lengths and P/N ratios of individual fish: no. 5, 18 cm and 0·63; no. 6, 16·5 cm and 0·62; no. 7, 9·5 cm and 0·67; no. 8, 13·7 cm and 0·83.

Fig. 4. Frequency difference *vs* response curves of four juvenile *Eigenmannia lineata*. ΔR and ΔF as defined in the legend to Fig. 1. These juvenile fish gave good responses to ΔFs of both signs (although frequency increase was stronger than decrease). Strongest responses were evoked by ΔFs close to and including zero. Their response curves appeared 'off centre' by $\Delta F \approx -0{\cdot}5$ Hz to −1 Hz. Each point is a mean ± 1 S.E. ($N = 12$). Standard errors are either shown or are too small to be drawn. Standard stimulus intensity. Body lengths and P/N ratios of individual fish: no. 1, 8·7 cm and 0·81; no. 2, 11 cm and 0·76; no. 3, 11 cm and 0·70; no. 4, 14·5 cm and 0·83.

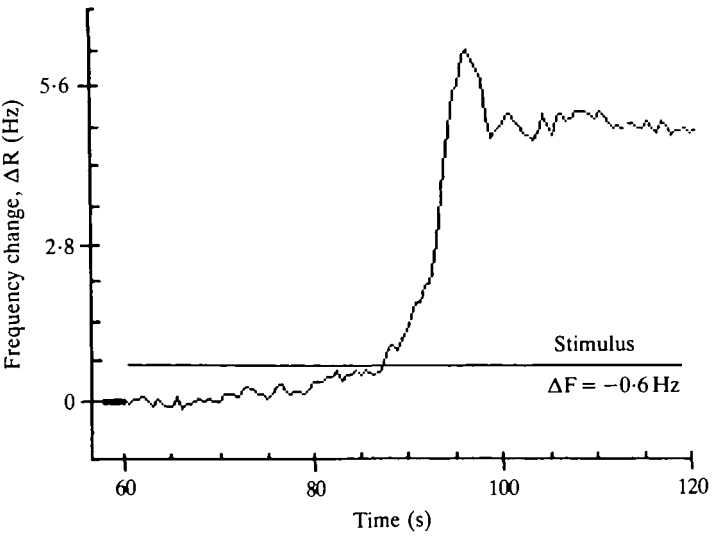

Fig. 6. Frequency change, ΔR, of juvenile no. 3 over time in response to ΔF = −0·6 Hz (single experiment, not averaged). Stimulus onset is at 60 s. Resting mean frequency (±1 S.D., based on 120 measurements during 60 s) shown at left. Although the fish should lower its frequency in order to increase the difference, it slowly raised its frequency and, after more than 25 s, skipped over it. Only then was a JAR evoked (although of opposite sign). Standard stimulus intensity.

One of these fish (no. 5) turned out to be female and was retested 2·25 years later (Fig. 8; results described in the next section). From the similarity among the response curves of juveniles nos 5–8 (Fig. 5), as opposed to those of juveniles nos 1–4 (Fig. 4), it is tentatively suggested that juveniles nos 5–8 are all immature females and nos 1–4 immature males (see also additional results at the end of this section).

It would be interesting to know whether juveniles nos 1–4 found their subjectively 'correct' responses to ΔF = 0 Hz (frequency increase; Fig. 4) by trial and error, since the crucial cue – beating of the stimulus frequency against the fish's EOD frequency (see Discussion) – was absent at the time of stimulus onset (below 0·01 Hz). Typical standard deviations of 1200 resting EOD intervals, sampled during the preceding minute, were below 0·5 μs at a mean of around 2000 μs in three out of these four fish; that is, the standard deviation was only 0·025 % of the mean (in the best cases, 0·008 %; in the worst case – one fish with an EOD interval of around 3400 μs – 0·168 %).

Juveniles nos 1–4 chose a positive ΔR (frequency increase) within 1·0–2·5 s after stimulus onset at ΔF = 0 Hz (the stimulus rise time of 0·4 s should be subtracted from this latency; Fig. 7). (Latency was defined as the time that the fish's EOD frequency remained within a frequency interval of ±1 standard deviation of its resting frequency after stimulation onset. With only two measurements per second these latencies are certainly overestimates.) The longest latency of an individual response – as opposed to the above values based on averaged curves – was 5 s ($N = 48$, four fish).

Response curves and latencies at $\Delta F = 0$ Hz were similar to those observed in response to ΔF values of 0·2 and 2·0 Hz (Fig. 7). At ΔF values of 0·2 and 2·0 Hz, latencies determined by averaging ($N = 12$) the response curves of each fish were 1·0–1·5 s, and up to 3·5 s for latencies in individual experiments ($N = 48$, four fish).

In contrast, the same four fish showed considerable uncertainty and, on average, no clear decision at $\Delta F = -0{\cdot}6$ Hz (juvenile no. 4: at $\Delta F = -1$ Hz; Fig. 7). Longest latencies in individual experiments exceeded the stimulation period of 60 s ($N = 36$, juveniles nos 1–3; 50 s in juvenile no. 4, $N = 12$).

Four recently obtained juvenile fish (apparently also *E. lineata*; two fish sexed by gonad histology) showed interesting similarities and differences from the above results (Figs 4, 5). A juvenile male (length, 8·5 cm; P/N ratio = 0·79) showed a near-maximal response to $\Delta F = 0$ Hz just like juveniles nos 1–4 (believed to be males);

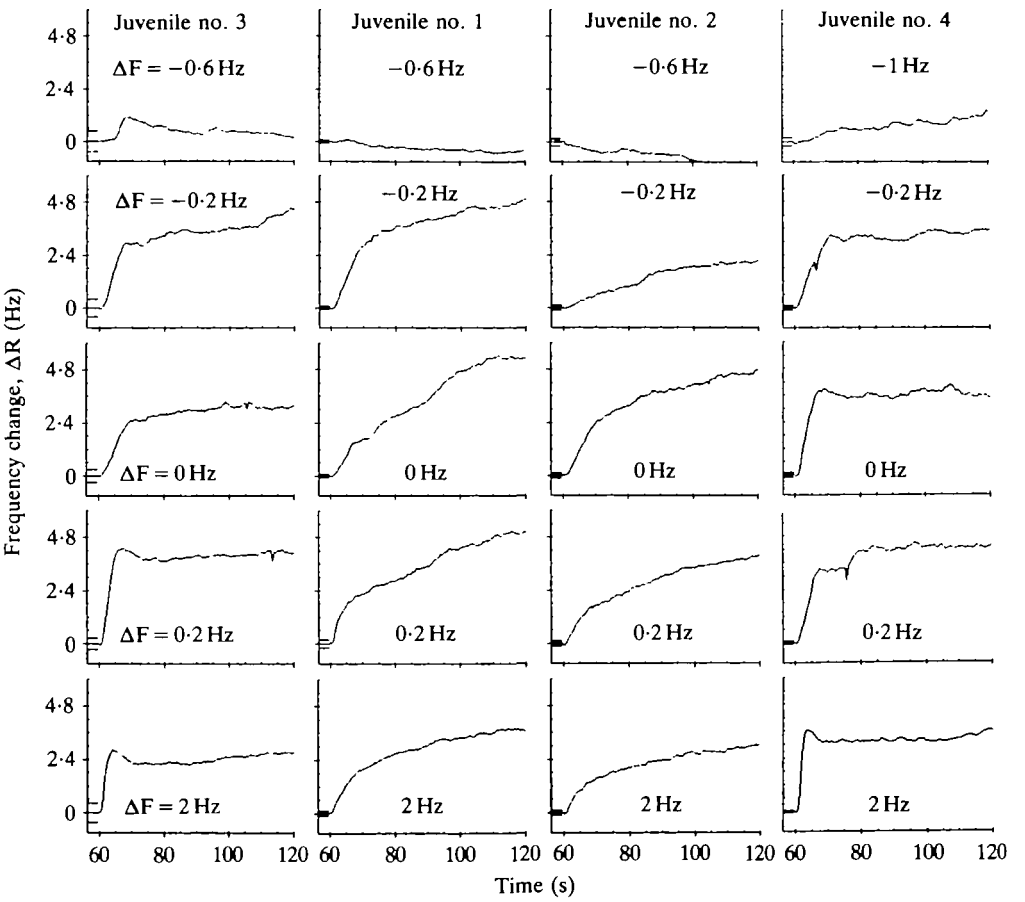

Fig. 7. Time courses of frequency changes, ΔR, in response to stimuli of various ΔF values in juveniles nos 1–4. Each curve is an averaged curve from 12 experiments. At $\Delta F = -0{\cdot}6$ Hz the fish were ambivalent in their choice of response direction, or did not respond at all (about −1 Hz in juvenile no. 4); at $\Delta F \geq -0{\cdot}2$ Hz, only positive ΔRs were evoked (including $\Delta F = 0$ Hz). Standard stimulus intensity.

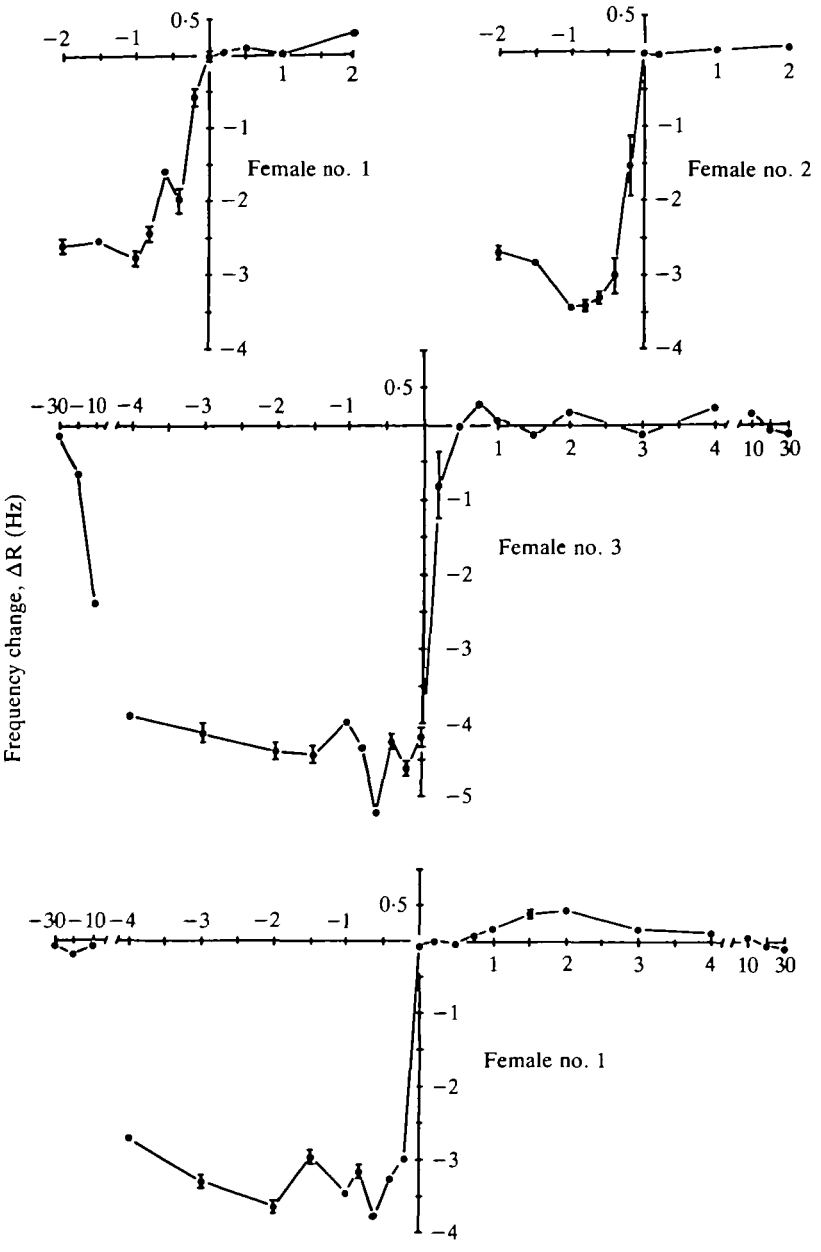

Fig. 8. Frequency difference *vs* response curves of three adult females, all gravid with eggs (female no. 1 retested 2·75 years later, below). ΔR and ΔF as defined in the legend to Fig. 1. Note that the females were almost insensitive to +ΔFs (including ΔF = 0 Hz, except female no. 3); −ΔFs evoked strong responses in all fish. Each point is a mean ± 1 S.E. ($N = 12$). Standard errors are either shown or are too small to be drawn. Standard stimulus intensity. Body lengths and P/N ratios of individual fish: female no. 1 (upper left), 15 cm and 0·61; female no. 1 (below, retested after 2·75 years), 15·5 cm and 0·60; female no. 2, 16 cm and 0·69; female no. 3, 18 cm and 0·63 (alias juvenile no. 5 of Fig. 5; 2·25 years separate the two observations).

however, its response was a frequency *decrease* instead of an increase ($-3{\cdot}39 \pm$ S.E. 0·12 Hz). It still significantly decreased its frequency in response to small $+\Delta$Fs (up to 0·75 Hz). Maximum responses were about ± 4 Hz. A juvenile female's (length, 11 cm; P/N ratio 0·82) frequency difference *vs* response curve was similar to that of juveniles nos 5–8 (Fig. 5; believed to be females) with the difference that $+\Delta$Rs were slightly stronger than $-\Delta$Rs. Two still unsexed fish (lengths, 8 and 9·6 cm; P/N ratios, 0·77 and 0·79, respectively) had frequency difference *vs* response curves resembling those of juveniles nos 5–8 (Fig. 5) (B. Kramer, unpublished results).

Frequency–response curves for adult fish

Adult females gravid with eggs ($N = 3$; body lengths 15, 16 and 18 cm) behaved in a qualitatively different manner from both kinds of juveniles in that they gave no responses (or only weak responses) to positive ΔF values; also $\Delta F = 0$ Hz was ineffective (except in female no. 3). Negative ΔF values elicited clear responses in all females (Fig. 8). Maximum responses were seen to ΔFs of $-0{\cdot}6$ to -2 Hz.

Juvenile no. 5 (P/N = 0·63), which could not be reliably sexed, matured into female no. 3 (P/N = 0·63). After 2·25 years in a big communal tank, where it had been kept together with one large male and a few smaller *Eigenmannia*, the fish had developed massive ovaries. When retested, the general shape of its response curve remained similar, although there are important differences between the behaviour of the mature and the immature fish: (1) the weak responses of the immature fish to $+\Delta$Fs were still weaker or lacking in the mature fish; (2) there was a strong response to $\Delta F = 0$ Hz in the mature fish (in contrast to the other mature females), which had been absent in the immature fish. While juveniles nos 1–4 gave frequency *increases* in response to $\Delta F = 0$ Hz, female no. 3 gave frequency *decreases* (Fig. 8; like one recently obtained juvenile male, see previous section). Thus, female no. 3 lowered its own frequency when the stimulus frequency was of equal (or slightly lower) frequency. This female's response latency of 1·0 s at $\Delta F = 0$ Hz (determined from an averaged response curve, $N = 12$) was within the latency range of juveniles nos 1–4 at $\Delta F = 0$ Hz; this is also true for the longest latency of an individual response of female no. 3, which was 3·0 s.

While there were considerable response differences related to sexual maturity in female no. 3 (alias juvenile no. 5), female no. 1 remained much more constant over 2·75 years (Fig. 8). Even at the time of the earlier measurement (P/N = 0·61), this fish had reached full sexual maturity, as was evident from her massively protruding ovaries in both instances (P/N = 0·60 at the time of the later measurement).

In females nos 1 and 3, weak responses were still obtained at $\Delta F = -20$ Hz ($P < 0{\cdot}001$); no responses were observed to ΔFs of ± 30 or ± 40 Hz (Fig. 8; lower two graphs).

Adult males (nos 1, 2 and 4, all >30 cm; and no. 3, 20·5 cm; P/N ratios $\leq 0{\cdot}50$, that is, typically male) showed a different response pattern (Fig. 9). The responses of these males were very weak or absent to any ΔF! While no consistent frequency increase in response to positive ΔF values was observed, there was a weak but consistent frequency decrease in response to negative ΔF values (except male no. 2,

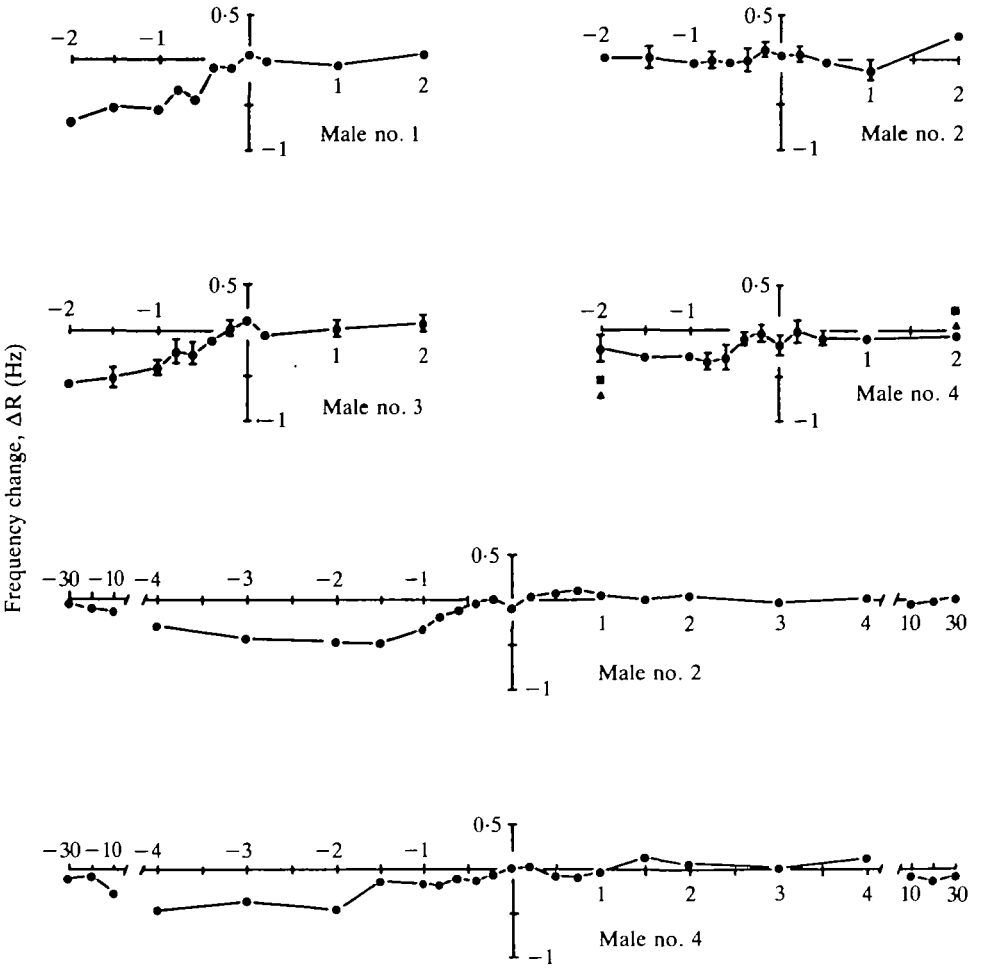

Fig. 9. Frequency difference *vs* response curves of four adult males (two males, lower two graphs, retested after 2·5 years). ΔR and ΔF as defined in the legend to Fig. 1. Note that the fish were insensitive to +ΔFs (including ΔF = 0 Hz); −ΔFs evoked only weak or no responses, which contrasts with the females' behaviour (Fig. 8). Each point is a mean ± 1 S.E. ($N = 12$). Standard errors are either shown or are too small to be drawn. Standard stimulus intensity except for the squares in the plot of male no. 4 (earlier measurement, upper right) which are +10 dB, and the triangles which are +20 dB. Body lengths and P/N ratios of individual fish: male no. 1, >30 cm (exact measurement not possible because of tail regeneration) and 0·42; male no. 2, 33·5 cm and 0·44; male no. 2 (retested after 2·5 years), 30 cm and 0·42; male no. 3, 20·5 cm and 0·50; male no. 4, 35 cm and 0·50; male no. 4 (retested after 2·5 years), 34 cm and 0·49.

which did not respond at all; first measurement). 2·5 years later males nos 2 and 4 still behaved in a very similar way (Fig. 9, lower two graphs; now there was a weak response to −ΔF in male no. 2). At ΔF = −20 Hz, a barely detectable response ($P < 0{\cdot}05$) was elicited in male no. 2, but not in male no. 4; ΔF = ±30 Hz or ±40 Hz was ineffective.

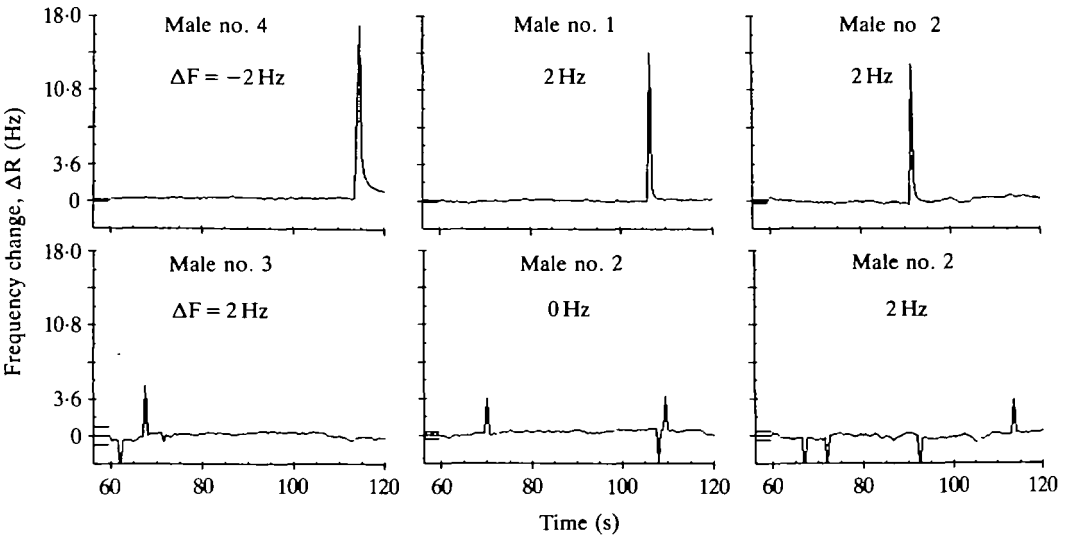

Fig. 10. Time course of frequency change, ΔR, in response to stimuli of various ΔF values in adult males (single experiments, not averaged). Although none of the fish gave a JAR, the stimuli elicited transient frequency modulations known from agonistic behaviour. Top: short rises of considerable strength; bottom: interruptions occurring together with short rises of weaker strength. Standard stimulus intensity.

Males are considerably larger and generate EODs (>100 mV_{P-P}, measured differentially head-to-tail) several times stronger than females (up to 16 mV_{P-P}); the intensity difference may approach a factor of 10 (Kramer, 1985). As *Eigenmannia* perceives the presence of a stimulus signal as the beating of the stimulus frequency against its own EOD frequency (Scheich & Bullock, 1974), the detection threshold could depend on the intensity ratio of the two signals. On this assumption the males' threshold should be several times higher than that of females, and males should give responses of normal strength to stronger stimuli.

The last part of this hypothesis is not, however, supported by the data. At a stimulus intensity 10 times the standard stimulus intensity (+20 dB) there was still no response to ΔF = +2 Hz (ΔR = 0·05 ± S.E. 0·05 Hz; $N = 12$; $P > 0{\cdot}05$), and only slightly stronger responses to ΔF = −2 Hz (−0·7 ± S.E. 0·08 Hz; $N = 12$; Fig. 9, male no. 4) compared with a stimulus of standard intensity.

There is, in contrast, evidence showing that males were very sensitive to the feeble signals of standard intensity, for they gave two categories of transient and rapid frequency modulations never given in the prestimulation period (although its duration was the same as that of the stimulation period; see Materials and Methods). These were the 'short rise' and a brief discharge cessation or pause, called 'interruption' (Fig. 10). The duration of a short rise was less than 2 s (after which the EOD frequency had dropped to about the same frequency as before); the duration of an interruption typically was 20–100 ms (Hopkins, 1974). An interruption was detected as a sharp frequency drop by the present methods (which were too slow to detect all interruptions or to measure their durations). The peak frequency change of

a short rise, as detected by the present methods, was of the order of at least 1 Hz but could be as big as 17·2 Hz (these values are underestimates for technical reasons: low sampling rate and averaging of 10 EOD cycles, see Materials and Methods; at a higher sampling rate of $3{\cdot}7\ s^{-1}$, short rises of up to 68·4 Hz from a resting frequency of 302·5 Hz were observed in male no. 2; B. Kramer, unpublished results). The three large males gave considerably more detectable short rises than interruptions (male no. 4 produced only short rises: $N = 28$), while the smaller male (no. 3) gave more detectable interruptions ($N = 21$) than short rises ($N = 8$; 144 JAR experiments per fish).

DISCUSSION

Types of jamming avoidance response

Watanabe & Takeda (1963) observed that the response, ΔR, to unclamped stimulus frequencies was 'very small, if present' when ΔF was more than ±20 Hz. This agrees with the present results.

However, the present group of 14 *Eigenmannia* showed four types of response to smaller ΔFs, associated with sex or age, not seen by Watanabe & Takeda (1963; results shown are from one fish) and Larimer & MacDonald (1968; one or two fish). It would be desirable to assess the inter-individual and possible geographical variability in more detail using a considerably larger number of fish, and to observe more closely the transformations which must take place during ontogenetic development. A precondition for this is a systematic revision of the genus *Eigenmannia* which is badly needed (see Kramer *et al.* 1981).

Adult males gave no responses or very weak ones (to −ΔF only); adult females gave good responses by frequency decrease to −ΔF, and no (or weak) responses to +ΔF. The most effective ΔFs in females (−0·6 to −2 Hz) were considerably greater in absolute terms than found by Watanabe & Takeda (1963) and Larimer & MacDonald (1968) (about 0·2–0·5 Hz). The great difference in response strength to negative ΔF values between males and females is not explained simply by lower absolute sensitivity of males resulting from their stronger EOD intensities, as shown by the use of stronger stimuli (Fig. 9).

A similar lack of responsiveness to ΔF values of one sign, and responsiveness to values of the opposite sign, is known from two gymnotoid wave fish, *Apteronotus (Sternarchus) leptorhynchus* (Larimer & MacDonald, 1968) and *Apteronotus albifrons* (Bullock *et al.* 1972*a*,*b*), but its functional significance (such as electroreception) has not been discussed. (In these apteronotids, only frequency *increases* in response to +ΔF and no, or only weak, frequency decreases in response to −ΔF were elicited.)

Sternopygus (of the same family as *Eigenmannia*, Sternopygidae) was reported to lack a JAR by Bullock, Behrend & Heiligenberg (1975, p. 117; 'a good many individuals' of unspecified size or sex were investigated) and Matsubara & Heiligenberg (1978; three adult, enucleated *S. macrurus* males; frequency changes of only up to ±0·5 Hz). As neither study provides data, it is not clear whether *Sternopygus*

displays only a weak, but statistically significant, response (like *Eigenmannia* males for $-\Delta F$ values, Fig. 9) or no response at all.

In juveniles nos 5–8, $+\Delta F$ stimuli elicited only a small change in frequency [much smaller than noticed by Watanabe & Takeda (1963) and Larimer & MacDonald (1968)]. Only juveniles nos 1–4 gave good responses to any ΔF within the effective range previously described. But even their behaviour differs from that described in the earlier studies: these juveniles still *increase* their EOD frequency at $-\Delta F$ (down to about $-0{\cdot}5$ Hz, and occasionally to $-1{\cdot}5$ Hz), when it would be more economical and faster to *decrease* EOD frequency to escape from the jamming stimulus frequency (one recently obtained juvenile male showed a frequency decrease in response to $\Delta F = 0$ Hz and small $+\Delta F$s, see Results).

Also, in contrast to the observations of Watanabe & Takeda (1963) and Larimer & MacDonald (1968), an increase in frequency was stronger than a decrease in these fish. This may be related to the asymmetry of the ΔR curves with respect to the abscissae: in increasing an initial frequency difference of, for example, $\Delta F = -1$ Hz by a response of $\Delta R = -2{\cdot}5$ Hz (a frequency decrease), a total frequency difference of $3{\cdot}5$ Hz results. That value is only obtained by a much greater increase in frequency of $\Delta R = +3{\cdot}7$ Hz in response to an initial ΔF of $-0{\cdot}2$ Hz (this ΔF value elicited only an increase in frequency, contrary to expectation).

Another puzzling aspect is that at $\Delta F = 0$ Hz, which was ineffective in the other fish (except female no. 3), juveniles nos 1–4 gave maximal responses ($+\Delta R$s). The frequency difference *vs* response curves given by Watanabe & Takeda (1963) and Larimer & MacDonald (1968) correspond best to those of these juveniles (present study), except that the responses to $\Delta F = 0$ Hz were not observed in the earlier studies (both mention some uncertainty of ΔF accuracy with their methods). Also, Bullock *et al.* (1972*a*,*b*) and Heiligenberg, Baker & Matsubara (1978) found $\Delta F = 0$ Hz to be ineffective (the number of fish on which this result is based is not clear in either of the studies). One may only speculate about the mechanisms and functions of this divergent behaviour ('strategies') in members of one species.

Mechanisms of divergent frequency change behaviour

It is clear from the present report that a specified ΔF, associated with a certain electroreceptor response pattern (see below), does not necessarily lead to one behavioural response pattern (JAR) in *Eigenmannia*: this would be expected if the only (or main) function of the JAR was to improve the signal-to-noise ratio for better electrolocation in the presence of stimuli of similar frequency (the signal here would be the fish's own EOD). The complex 'block diagram of components in the JAR system' (Bullock *et al.* 1972*b*; their fig. 11) offers at least two boxes where such differences might reside: the box named 'activity command' (representing a heterogeneous command for EOD frequency changes of unclear origin) and the box named 'limiter'. The properties of the limiter would enable the adult females, for example, not to respond to $+\Delta F$ in spite of their responsiveness to $-\Delta F$ (Fig. 8).

I suggest that the diagram should provide for a variable limiter as adult females occasionally gave JARs (frequency *increase*) to computer-synthesized male EODs at

$+\Delta F$ (Kramer, 1985). A variable limiter is also needed to provide for the presumed transitions of the juvenile to subadult, and subadult to adult response types, in part observed in female no. 3 alias juvenile no. 5 (Figs 5, 8).

While some kind of a limiter may explain the adult fishes' unresponsiveness to $+\Delta F$ (in males, $-\Delta F$ was also almost or totally ineffective), no immediate explanation is at hand for the juveniles' (nos 1–4, Fig. 4; and an additional one probably from a different locality) and one female's (no. 3; Fig. 8) strong responses to $\Delta F = 0$ Hz, which has always been thought to be an ineffective stimulus. For $\Delta F = 0$ Hz, theory specifically predicts no JAR as there is no periodic variation in the combined signal (EOD superimposed by the stimulus). The presumed electrolocation performance, as studied by an overt, spontaneous following response to moving objects, was unimpaired under a jamming stimulus sufficiently close to $\Delta F = 0$ Hz (Matsubara & Heiligenberg, 1978).

In theory, the fish's EOD serves as a kind of 'carrier' frequency which is modulated by the stimulus signal in amplitude and phase at the beat frequency, that is the frequency difference. Electroreceptors of two types are sensitive to these periodic variations within a beat cycle: P-receptors (probability of firing) reflect the amplitude envelope of the beating field, and T-receptors (phase of the 1:1 spike) reflect the phase modulations of zero-crossings within a beat. Hence both receptor types transmit information on ΔF. The fish could distinguish $+\Delta F$ from $-\Delta F$ by comparison of the time courses of amplitude and phase modulations of the beating field; true frequency analysis seems unlikely (Scheich & Bullock, 1974; Scheich, 1974, 1977*a*,*b*,*c*).

The sign of ΔF could be determined from these electroreceptor responses in two ways: (1) by analysis of the amplitude envelopes of the beat patterns which – because of the harmonic content of the EOD – are time-asymmetric mirror images for identical ΔF values of opposite sign (Scheich, 1974, 1977*a*,*b*,*c*), and (2) by comparing P- and T-receptor responses from different skin areas and detecting a kind of 'motion' as specified in an amplitude–phase state–plane model, or Lissajous figure (reviewed in Heiligenberg, 1986). (The motion in this model is of opposite direction for $+\Delta F$ and $-\Delta F$.)

An explanation of the juveniles' (nos 1–4; and one additional juvenile male) and one female's (no. 3) responsiveness to $\Delta F = 0$ Hz (present report) might be that random fluctuations of their EOD rates (although very small, see Results; and Bullock *et al.* 1975, p. 118) trigger the response. Once there is a frequency difference, however small, this would elicit the response. This explanation cannot be ruled out on the basis of the present experiments (but see below, and Fig. 11). However, the explanation seems insufficient since the frequency change was always in the same direction without detectable delay (frequency increase in the case of juveniles nos 1–4, frequency decrease in female no. 3 and an additional juvenile male). Frequency change in both directions and delay – at least occasionally – should be observed if the 'random frequency fluctuation hypothesis' was to be applied. This has been observed in the unrelated African mormyriform fish with a similar wave discharge, *Gymnarchus niloticus*, which, in contrast to *Eigenmannia*, commonly shows

irregular fluctuations in EOD frequency and 'singing' (Bullock *et al.* 1975; their figs 2A–C, 3), and spontaneous and stimulation-evoked discharge stops (Szabo & Suckling, 1964).

Juveniles nos 1–4 showed the behaviour expected at $\Delta F = 0$ Hz only at $\Delta F = -0{\cdot}6$ Hz to -1 Hz (Figs 4, 6, 7): the fish (a) delayed choosing the sign of their response or (b), often in addition, chose to change their frequency in the wrong direction or (c) did not respond at all ($|\Delta R| < 0{\cdot}3$ Hz; similar to the averaged response, Fig. 7).

Does this mean the fish were unable to determine the correct sign of ΔF, although at $\Delta F = -0{\cdot}6$ Hz there was one beat cycle per 1·67 s? (One-quarter of a beat cycle, 0·42 s in this case, is sufficient for the fish to determine ΔF; Bullock *et al.* 1972*b*.) How could the fish quickly and consistently respond to stimuli of $\Delta F = 0$ Hz in the absence of a detectable frequency difference (see Materials and Methods)? Also, the human eye – observing the beat frequency – could not detect relative movement between the stimulus, adjusted to the EOD frequency by computer (see Materials and Methods), and the EOD, displayed on separate traces of the oscilloscope triggered by the EOD of an unstimulated fish, for at least several seconds (except in rare cases). Occasionally, the stimulated fish still changed their frequency in the 'wrong' direction at $\Delta F = -0{\cdot}8$ Hz (one beat cycle per 1·25 s), and juvenile no. 4 even at $\Delta F = -1{\cdot}5$ Hz (one beat cycle per 0·67 s). From the uncertainty about which sign the response would take at $\Delta F = -0{\cdot}6$ Hz, the accuracy of assessment of ΔF is not better than $\pm 0{\cdot}3$ Hz.

At $\Delta F = 0$ Hz, cues not yet identified must enable the fish to respond in a predictable way. This is not to deny that once a certain threshold frequency difference is reached, the response might be maintained by amplitude and phase modulations of the combined field beating at increasingly higher frequencies as the fish continues to change its frequency.

A JAR can even be evoked in the maintained absence of beating of the fish's EOD field, by the use of a frequency-clamp set at $\Delta F = 0$ Hz (B. Kramer, unpublished results). A slightly time-asymmetric square wave (that is, one half-wave shorter than the other, to allow for frequency increase), triggered cycle per cycle by the fish's EOD, evoked a strong and immediate frequency increase, but only at certain phases relative to the EOD (for example, on average 0·9 Hz at $\phi = 75°$ phase difference relative to the positive-going zero-crossing of the EOD; Fig. 11). This frequency increase was immediately followed by a decrease to about 0·4 Hz above resting frequency. In this experiment with juvenile no. 1, ΔF was strictly maintained at 0 Hz during the fish's response.

One possible cue enabling the fish to respond to $\Delta F = 0$ Hz is a noise-like pulse of broad spectral composition associated with sudden stimulus onset, although this could give information only about the time of stimulus onset, and not about ΔF. It might still cause the fish to give a frequency change (even a systematic one) and thus trigger the JAR. This explanation is unlikely, however, because of the 'soft' stimulus onset (rise time 400 ms) and the low stimulus intensity used in the present experiments. The rise time is not specified in any of the earlier studies.

A more likely cue is a step-like change of the fish's perceived EOD amplitude (at least in those parts of its skin where the stimulus gradient is maximal) at stimulus onset. This hypothesis is supported by the observation of frequency drops of up to 4·5 Hz in response to sudden changes of environmental resistance (hence perceived EOD amplitude) in *Eigenmannia* (Larimer & MacDonald, 1968; their fig. 9). A step-like amplitude change of the EOD is also caused by superposition with a wave-signal of identical frequency.

An amplitude change should be perceived by P-receptors; T-receptors should perceive the change of phase of the voltage gradient crossing the zero-line and might respond even if just the slope of that gradient changed in the absence of any change of phase.

The amplitude change caused by a stimulus of $\Delta F = 0$ Hz can be an increase or a decrease, depending on the phase difference, and should lead to opposite changes of the response patterns of P- and T-receptors. Stimulus phase was not controlled in the present experiments (except those shown in Fig. 11); therefore, stimuli of all phases were probably used. In spite of this, there was only one response pattern per fish (juveniles nos 1–4, female no. 3 and an additional juvenile male). Phase-locked stimuli of all phases had been found ineffective by Watanabe & Takeda (1963), Bullock *et al.* (1972*b*) and Heiligenberg *et al.* (1978). This is probably due to the very small number of fish studied without reference to sex or age groups.

An alternative – or additional – explanation of the sensitivity of a group of juveniles and of female no. 3 (present report) to stimuli of $\Delta F = 0$ Hz involves the ampullary

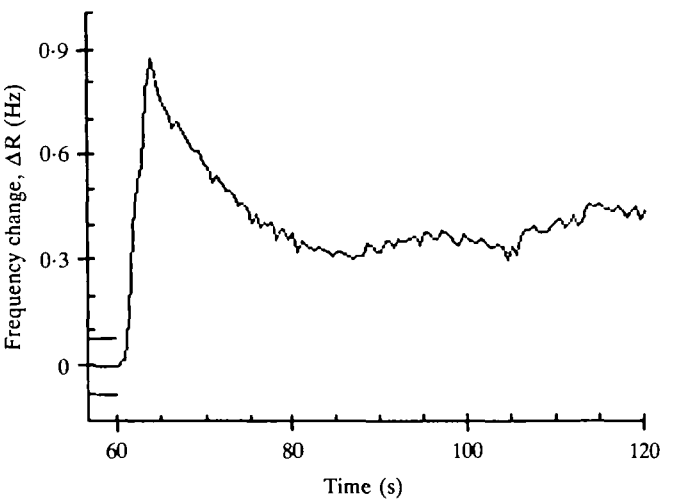

Fig. 11. As Fig. 6, but for juvenile no. 1 (average curve from 12 experiments). In contrast to all other experiments, a biphasic square-wave stimulus was phase-locked to the fish's EOD, that is ΔF was also set at 0 Hz during the fish's response. Square wave of standard intensity; slightly time-asymmetric to allow for frequency increase of the function generator in the event of an EOD frequency increase (in order to maintain $\Delta F = 0$ Hz). The phase difference relative to the positive-going EOD zero-crossing was 75°. Note strong frequency change although there was no periodic modulation of the EOD by the stimulus.

electroreceptors with their acute low-frequency sensitivity (reviews by Szabo & Fessard, 1974; Bullock, 1982). A step-like EOD amplitude change should be clearly sensed by these receptors. The suggestion of Bullock *et al.* (1972*b*) that ampullary receptors might play a role in the JAR by sensitivity to the low-frequency beat envelope has not been investigated.

Functions of the divergent frequency change behaviour

Although the JAR has never been observed in nature, there exist a few laboratory observations of two-fish interactions (Bullock *et al.* 1972*a*,*b*; not fully documented), and experiments on the effect of artificial, jamming stimuli on an unconditioned, overt following behaviour presumably mediated by the electric sense (for reviews see Heiligenberg, 1977, 1986). Heiligenberg concludes that the JAR is part of an 'early warning system', enabling the fish to shift to a safer frequency, long before an approaching intruder with similar EOD frequency can disrupt its electrolocation.

EOD frequency modulations during social behaviour have been described in *E. virescens* (Hopkins, 1974; Hagedorn & Heiligenberg, 1985). The time course of one kind of modulation, the 'long rise', resembles a JAR given to $+\Delta F$. Is the reason adult *Eigenmannia* do not give JARs to $+\Delta F$ the similarity of that response to the long rise signalling submission or retreat? (Adult females stimulated with computer-synthesized male EODs of $+\Delta F$ sometimes gave a $+\Delta R$; Kramer, 1985.)

The reason adult males do not (or only weakly; Fig. 9) respond to $-\Delta F$ is not known; in nature, adult males are unlikely placidly to give JARs on encountering a conspecific with jamming EOD frequency, as they are extremely aggressive, chasing away conspecifics. Vicious fights are the rule, especially with other large males, followed by prolonged, high-intensity chasing of the loser by the winner, so that the fish have to be separated (360-l aquaria of 60×120 cm bottom area). The males of the present study often gave short rises and interruptions (Fig. 10) in response to the jamming signals, categories of transient EOD frequency modulations observed in threatening fish likely to attack (Hopkins, 1974).

The chance that adult males might meet conspecifics of similar frequency (except large males) seems low, since the frequencies of all four adult males (>30 cm) were at the low end (268–364 Hz; Kramer, 1985) of the species' frequency distribution (260–650 Hz at 27°C for *E. virescens* with which *E. lineata* has apparently often been confused; Hopkins, 1974; Westby & Kirschbaum, 1981). The EOD intensity of adult males (100 mV_{P-P} head-to-tail, or more) is so much higher than that of the other sex or age groups (up to 16 mV_{P-P}; Kramer, 1985) that these fish, on meeting an adult male of suitable EOD frequency, would give a response long before the adult male (for stimulus intensity *vs* response relationship see Kramer, 1985).

It is unlikely, however, that adult males would elicit JARs in adult females, as these only respond to frequencies higher than their own (Fig. 8). If, however, the male happened to display a frequency closely above half the female's a JAR would be elicited, as the strong second harmonic of the male EOD would be close to the fundamental frequency of the female's EOD (Kramer, 1985). A male discharging at half the female's frequency is probably not rare in nature (for evidence see Kramer,

1985). Whether such a response would be of social significance is impossible to ascertain from the present results. *Eigenmannia* discriminates synthetic male from female resting EODs in the absence of amplitude or frequency cues (Kramer & Zupanc, 1986).

The behaviour of all four groups of individuals – especially adult fish – appears more or less maladapted, because a symmetrical frequency difference *vs* response curve with strongest responses for smallest ΔFs (which no group showed) would be optimal for electrolocation in the presence of jamming stimuli. It is doubtful, however, whether electrolocation performance often suffers under natural conditions when a JAR would be elicited. Presumed electrolocation performance, as measured by a spontaneous, unrewarded following behaviour to moving objects, deteriorated only when the intensity of a jamming stimulus approached the fish's own near-field EOD intensity (Heiligenberg, 1977). To experience such high intensities from another fish's EOD field, two fish of comparable size (and almost identical EOD frequency) must be very close to each other (Heiligenberg, 1977, gives 4 cm; his fig. 34). From aquarium and field observations such instances are rare (except during fighting or courtship, when a JAR is unlikely because of the presence of other kinds of frequency modulations; see above).

The electrolocation performance of *Sternopygus* males, which did not show a JAR, was only impaired at an unphysiologically high stimulus intensity of 50 times their own near-field EOD intensity ($2{\cdot}5\,mV\,cm^{-1}$; Matsubara & Heiligenberg, 1978). This immunity of *Sternopygus* to jamming stimuli gave rise to an alternative hypothesis of how an electric fish might detect moving objects in the presence of jamming stimuli (briefly reviewed in Heiligenberg, 1986): the spatial pattern of amplitude modulations of the fish's own EOD caused by small, moving objects certainly differs from the more global ones caused by a distant dipole current source, such as a conspecific. This difference might enable the fish to distinguish between the two kinds of disturbances. This hypothesis might well also apply to *Eigenmannia*, the adult males of which did not show a JAR (or only one considered to be too small to be called a JAR in *Sternopygus*).

Also, the observation of strong JARs (Figs 4, 8, 11) of some of the fish to stimuli of $\Delta F = 0\,Hz$ (which do not impair electrolocation performance; Matsubara & Heiligenberg, 1978), of strong habituation (Fig. 3), and of a disconcertingly high inter- (and sometimes intra-) individual and probably geographical variability do not suggest that the JAR is important in electrolocation.

This shows that we know little about the function(s) (and mechanisms, see previous section) of the JAR, and about the selective forces which shaped the response (such as those probably imposed by the other function of the electric system – communication). However, I suggest that the name of the JAR should not be changed, until the true function has been securely established.

The JAR could have acquired functions other than the ones it originally served (through evolutionary change as described by the ethological concepts of ritualization and emancipation; see, for example, Manning, 1978), as it could clearly have

been a preadaptation (see, for example, Wilson, 1975) for social signalling by frequency modulations. Investigations into the social behaviour and individual life histories should help clarify some of the obscure points.

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REFERENCES

BULLOCK, T. H. (1982). Electroreception. *A. Rev. Neurosci.* **5**, 121–170.

BULLOCK, T. H., BEHREND, K. & HEILIGENBERG, W. (1975). Comparison of the jamming avoidance responses in gymnotoid and gymnarchid electric fish: a case of convergent evolution of behavior and its sensory basis. *J. comp. Physiol.* **103**, 97–121.

BULLOCK, T. H., HAMSTRA, R. H. & SCHEICH, H. (1972*a*). The jamming avoidance response of high frequency electric fish. I. General features. *J. comp. Physiol.* **77**, 1–22.

BULLOCK, T. H., HAMSTRA, R. H. & SCHEICH, H. (1972*b*). The jamming avoidance response of high frequency electric fish. II. Quantitative aspects. *J. comp. Physiol.* **77**, 23–48.

HAGEDORN, M. & HEILIGENBERG, W. (1985). Court and spark: electric signals in the courtship and mating of gymnotoid fish. *Anim. Behav.* **33**, 254–265.

HEILIGENBERG, W. (1977). *Principles of Electrolocation and Jamming Avoidance in Electric Fish. Studies of Brain Function*, vol. 1. Berlin, Heidelberg, New York: Springer-Verlag.

HEILIGENBERG, W. (1986). Jamming avoidance responses: model systems for neuroethology. In *Electroreception* (ed. T. H. Bullock & W. Heiligenberg), pp. 613–649. New York, Chichester, Brisbane, Toronto, Singapore: John Wiley & Sons.

HEILIGENBERG, W., BAKER, C. & MATSUBARA, J. (1978). The jamming avoidance response in *Eigenmannia* revisited: the structure of a neural democracy. *J. comp. Physiol.* **127**, 267–286.

HOPKINS, C. D. (1974). Electric communication: functions in the social behavior of *Eigenmannia virescens*. *Behaviour* **50**, 270–305.

HOPKINS, C. D. (1976). Stimulus filtering and electroreception: tuberous electroreceptors in three species of gymnotoid fish. *J. comp. Physiol.* **111**, 171–207.

KIRSCHBAUM, F. & WESTBY, G. W. M. (1975). Development of the electric discharge in mormyrid and gymnotid fish (*Marcusenius* sp. and *Eigenmannia virescens*). *Experientia* **31**, 1290–1293.

KRAMER, B. (1985). Jamming avoidance in the electric fish *Eigenmannia*: harmonic analysis of sexually dimorphic waves. *J. exp. Biol.* **119**, 41–69.

KRAMER, B., TAUTZ, J. & MARKL, H. (1981). The EOD sound response in weakly electric fish. *J. comp. Physiol.* **143**, 435–441.

KRAMER, B. & WEYMANN, D. (1987). A microprocessor system for the digital synthesis of pulsed or continuous discharges of electric fish (or animal vocalizations). *Behav. Brain Res.* **23**, 167–174.

KRAMER, B. & ZUPANC, G. K. H. (1986). Conditioned discrimination of electric waves differing only in form and harmonic content in the electric fish, *Eigenmannia*. *Naturwissenschaften* **73**, 679–680.

LARIMER, J. L. & MACDONALD, J. A. (1968). Sensory feedback from electroreceptors to electromotor pacemaker centers in gymnotids. *Am. J. Physiol.* **214**, 1253–1261.

MANNING, A. (1978). *An Introduction to Animal Behaviour*, 3rd edn. London: Edward Arnold.

MATSUBARA, J. & HEILIGENBERG, W. (1978). How well do electric fish electrolocate under jamming? *J. comp. Physiol.* **125**, 285–290.

SACHS, L. (1978). *Angewandte Statistik. Statistische Methoden und ihre Anwendungen*. Berlin, Heidelberg, New York: Springer-Verlag.

SCHEICH, H. (1974). Neural analysis of waveform in the time domain: Midbrain units in electric fish during social behavior. *Science* **185**, 365–367.

SCHEICH, H. (1977*a*). Neural basis of communication in the high frequency electric fish, *Eigenmannia virescens* (jamming avoidance response). I. Open loop experiments and the time domain concept of signal analysis. *J. comp. Physiol.* **113**, 181–206.

SCHEICH, H. (1977*b*). Neural basis of communication in the high frequency electric fish, *Eigenmannia virescens* (jamming avoidance response). II. Jammed electroreceptor neurons in the lateral line nerve. *J. comp. Physiol.* **113**, 207–227.

SCHEICH, H. (1977*c*). Neural basis of communication in the high frequency electric fish, *Eigenmannia virescens* (jamming avoidance response). III. Central integration in the sensory pathway and control of the pacemaker. *J. comp. Physiol.* **113**, 229–255.

SCHEICH, H. & BULLOCK, T. H. (1974). The detection of electric fields from electric organs. In *Handbook of Sensory Physiology*, vol. III/3 (ed. A. Fessard), pp. 201–256. Berlin, Heidelberg, New York: Springer-Verlag.

SCHEICH, H., BULLOCK, T. H. & HAMSTRA, R. H., JR (1973). Coding properties of two classes of afferent nerve fibres: High frequency electroreceptors in the electric fish, *Eigenmannia*. *J. Neurophysiol.* **36**, 39–60.

SCHEICH, H. & EBBESSON, S. O. E. (1983). Multimodal torus in the weakly electric fish *Eigenmannia*. *Advances in Embryology and Cell Biology*, vol. 82. Berlin, Heidelberg, New York, Tokyo: Springer-Verlag.

SIEGEL, S. (1956). *Nonparametric Statistics for the Behavioral Sciences*. New York; McGraw-Hill.

SZABO, T. & ENGER, P. S. (1964). Pacemaker activity of the medullary nucleus controlling electric organs in high frequency gymnotid fish. *Z. vergl. Physiol.* **49**, 285–300.

SZABO, T. & FESSARD, A. (1974). Physiology of electroreceptors. In *Handbook of Sensory Physiology*, vol. III/3 (ed. A. Fessard), pp. 59–124. Berlin, Heidelberg, New York: Springer-Verlag.

SZABO, T. & SUCKLING, E. E. (1964). L'arrêt occasionel de la décharge électrique continue du Gymnarchus est-il une réaction naturelle? *Naturwissenschaften* **51**, 92.

VIANCOUR, T. A. (1979*a*). Electroreceptors of a weakly electric fish. I. Characterization of tuberous electroreceptor tuning. *J. comp. Physiol.* **133**, 317–325.

VIANCOUR, T. A. (1979*b*). Electroreceptors of a weakly electric fish. II. Individually tuned receptor oscillations. *J. comp. Physiol.* **133**, 327–338.

VIANCOUR, T. A. (1979*c*). Peripheral electrosense physiology: a review of recent findings. *J. Physiol., Paris* **75**, 321–333.

WATANABE, A. & TAKEDA, K. (1963). The change of discharge frequency by a.c. stimulus in a weak electric fish. *J. exp. Biol.* **40**, 57–66.

WESTBY, G. W. M. & KIRSCHBAUM, F. (1981). Sex differences in the electric organ discharge of *Eigenmannia virescens* and the effect of gonadal maturation. In *Sensory Physiology of Aquatic Lower Vertebrates. Adv. Physiol. Sci.*, vol. 31 (ed. T. Szabo & G. Czeh), pp. 179–194. Budapest: Pergamon Press/Akademiai Kiado.

WILSON, E. O. (1975). *Sociobiology. The New Synthesis*. Cambridge MA: Belknap Press.

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